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Title: Relationships Of The Freshwater Naiad *Margaritifera margaritifera falcata* to Some Fishes Of The Willamette River

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Smolt and presmolt coho salmon (*Oncorhynchus kisutch*), chinook salmon (*Oncorhynchus tshawytscha*), and steelhead trout (*Salmo gairdneri*) were compared for glochidial susceptibility to *Margaritifera margaritifera falcata*. A student's "t" test showed chinook salmon presmolts and smolts were the most susceptible hosts followed by steelhead trout presmolts and coho salmon presmolts. Susceptibility differences between coho and steelhead presmolts, and chinook and steelhead smolts, were less distinct. Steelhead presmolts were more susceptible hosts than coho presmolts at lower glochidial exposure concentrations but not at the higher concentrations. Chinook smolts were also more susceptible than steelhead smolts at the lower glochidial exposure concentrations but not at the higher concentrations. A physiological reaction was suspected as the cause for the reversals in susceptibility to infection. No clear

differences in infectibility were evident in comparing smolts to presmolts in chinook, coho, and steelhead.

Glochidia affected the condition factor of all infected salmonids. Fish harboring high glochidial numbers showed greater declines in condition factor than those with low glochidial numbers 10 days post infection. Control fish generally showed increases in condition factor after 10 days. Exposed fish showed no increases.

The torrent sculpin (*Cottus rhotheus*) was successfully infected artificially with *M. m. falcata* glochidia. Natural infections were noted in the chinook salmon (*Oncorhynchus tshawytscha*), prickly sculpin (*Cottus asper*), torrent sculpin (*C. rhotheus*), longnose dace (*Rhinichthys cataractae*).

A method for artificially spawning *M. m. falcata* was partially successful.

Relationships of the Freshwater Naiad *Margaritifera margaritifera falcata* to Some Fishes of the Willamette River

by

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INTRODUCTION

The glochidia of the freshwater naiad (Unionidae) *Margaritifera margaritifera falcata* infect and encyst in gills of salmonid fishes (Riedl, 1928; Murphy, 1942), but host specificity and chronology of the glochidial encystment in the gills of fishes has not been thoroughly documented. Resident fish such as the mountain whitefish, *Prosopium williamsoni*, and the Piute sculpin, *Cottus bairdi*, appear resistant to glochidial infections of *M. m. falcata* (Murphy, 1942). However, coho salmon, (*Oncorhynchus kisutch*), and chinook salmon (*Oncorhynchus tshawytscha*, show distinct differences in susceptibility to glochidial infections (Karna, 1973). Differences in the blood composition appear to be the basis for host resistance (Meyers, 1975; Fustish, 1976). Coho salmon slough the glochidia from the gills in a short period, but the glochidia mature to the juvenile stage in the gills of the chinook salmon.

Resistance to infection of glochidia may be more important in resident fish than in anadromous fish. Repeated glochidial infections could decrease the physical condition of fish. Resistance to infection of glochidia might decrease the mortality rate in a population of resident fish. Meyers (1975) compared the susceptibility of steelhead trout and cutthroat trout, (Salmo clarki), and found cutthroat were more resistant to the glochidia of M. m. falcata but there is insufficient evidence to document a difference in susceptibility to glochidia between anadromous and resident fishes. Susceptibility differences might explain glochidia movements downstream and clarify the mechanisms causing the wide geographic distribution of the naiad.

The ability of smolts and presmolts to avoid infections may be a factor causing different survival rates in coho salmon, chinook salmon, and steelhead trout. Experimental infections with glochidia have been conducted with juvenile fishes (Meyers, 1975), but the smolting stage in anadromous fish has not been subjected to glochidial infections. Smolts appear to be physiologically different from presmolts and offer an opportunity to compare susceptibility to glochidia between smolts and presmolts. A preference for smolts will help distribute the naiad downstream.

Glochidial effects on the growth and condition of coho salmon, chinook salmon, and steelhead are lacking. Heavy loads of glochidia on the gills may lower the condition factors of fish and have an effect on smolts adjusting to the marine environment. Additionally, all the fish hosts of M. m. falcata are not known. Margaritifera margaritifera is found over a wide geographic range and the subspecies *Margaritifera margaritifera* falcata is found in the western United States. Several species of fish probably serve as glochidial hosts. Potential host species of fish need to be determined. New resident hosts would help explain how naiad populations are maintained or moved upstream.

Margaritifera spawns only in the spring limiting the time available for productive research on the glochidia. A laboratory technique for obtaining gametes is needed so that experiments with glochidia can be conducted throughout the year.

The primary objectives of this investigation were: (1) to experimentally determine the relative susceptibility of smolts and presmolts of chinook salmon, coho salmon, and steelhead trout to the glochidial infections of *M. m. falcata*; (2) to measure the effect of glochidial infections on the growth and condition factors of the three salmonid species. Secondary objectives included: the examination of non-salmonid fish as possible hosts for glochidia of *M. m. falcata*, and an attempt to establish an artificial method for spawning *M. m. falcata*.

LITERATURE REVIEW

Range

The range of the freshwater naiad *Margaritifera margaritifera* is holarctic. It is abundant in Scandanavia and western North America (Roscoe and Redelings, 1964). In North America this species occurs from Newfoundland to about latitude 40°N on the east coast, and from Naka Bay, Alaska to about 35°N on the west coast (Dall, 1905; Walker, 1910; Jackson, 1925; Roscoe and Redelings, 1964). Ingram (1948) determined the general range of the subspecies *Margaritifera margaritifera falcata* in Washington, Oregon, and California. The species distribution in Oregon is incomplete because many coastal and inland streams have not been surveyed (Karna, 1973).

Ecology

Naiads customarily inhabit stream bottoms free of rooted vegetation with stable gravel, sand, and substrates composed of sand or gravel mixed with other materials (Pennak, 1953). Hendelberg (1960) found *M. margaritifera* in cool, swift flowing waters, which are low in dissolved calcium carbonate, and in fast currents behind boulders in central and northern Europe. Roscoe and Redelings (1964) reported a naiad bed in Kettle River near Barstow, Washington confined to an area of swift water flow; the water depth ranged from 0.6-1.2 m at the lowest level, and the substrate consisted mainly of boulders, gravel, and sand. Murphy (1942) reported the species generally remain stationary but Jackson (1925) reported movements of 4.5 m per day under favorable water conditions.

Life History

During late April or early May, eggs in the female pass from the ovaries via the suprabranchial chamber to the marsupia in the gills where fertilization occurs from sperm that enter through the incurrent siphon (Lefevre and Curtis, 1912). The development from unfertilized eggs to mature larvae takes from 16-28 days depending on the water temperature (Jackson, 1925; Riedl, 1928). Murphy (1942) stated that development takes 12 days at 13.1°C. Mature glochidia are expelled into the water and must come in contact with a suitable fish host before falling to the stream bottom to continue development. The nonswimming glochidia enter the fishes mouth with the respiratory current and in the opercular cavity attach by valve contraction to the gill lamellae and gill filaments (Riedl, 1928). The glochidia of _M_. _m_. _falcata_ have six or seven minute teeth on the ventral rim of the calcareous shell that aids in attachment (Jackson, 1925). Rainbow trout and brown trout (_S_. _trutta_) retain the encysted glochidia for 36 days at a water temperature of 14°C (Murphy, 1942). Karna (1973) found M. m. falcata increased 500% in size during metamorphosis while Murphy (1942) reported an increase of 600%. When metamorphosis is completed, the cyst wall is ruptured by the foot of the young naiad and the bivalve falls to the substrate bottom. The naiad settles on the stream bottom and attaches to the bottom debris by byssal threads. The byssus is lost when the naiad attains a length of 50 mm (Murphy, 1942). M. m. falcata reaches sexual maturity at approximately 30 mm in length (Murphy, 1942) and the sexes are usually separate (Hendelberg, 1960).

Host Specificity

There are reports of natural immunity of some fish species to glochidiosis. Lefevre and Curtis (1912) stated the hookless glochidia of L. ligamentina and Symphynota complanata were unable to invade the gills of largemouth bass (Micropterus salmoides). Murphy (1942) reported mountain whitefish and sculpins were resistant to M. m. falcata infection. Recently Karna (1973) reported a marked difference in susceptibility between coho salmon and chinook salmon 40-50 mm in length with coho more resistant. Differences in blood and mucus composition seem to be the basis for differences in susceptibility and for host resistance (Fustish, 1976). A more detailed account of this in *M. m. falcata* is given by Meyers (1975). The interrelationships between glochidia and anadromous and non anadromous fish and also smolt and presmolt fishes may show why one group is more resistant to the glochidia than the other. It may be advantageous for the glochidia to prefer a smolt or anadromous fish instead of a presmolt or non anadromous fish. Smolt preference would enable the naiad to be moved downstream. This may help explain the wide geographic range of *M. m. falcata*.

MATERIAL AND METHODS

Experimental fishes came from several sources. Smolts and presmolts of steelhead trout and chinook presmolts were provided by the U.S. Environmental Protection Agency's Western Fish Toxicology Laboratory in Corvallis, Oregon. The chinook smolts were raised at Oregon State University. The coho smolts were obtained from the Oregon Department of Fish and Wildlife's Trask River Hatchery and the coho presmolts came from the Oregon Department of Fish and Wildlife's Fall Creek Hatchery. Total length for each species and developmental stages were: coho presmolts, 40-60 mm; chinook presmolts, 40-80 mm; steelhead presmolts, 15-30 mm; coho smolts, 90-120 mm; chinook smolts, 110-130 mm; steelhead smolts, 100-125 mm.

Smolt and Presmolt Susceptibilities

Gravid *M. m. falcata* were obtained from the west bank of the Willamette River near Smith Loop, 3.2 km S.W. of Peoria. Water temperature was 9.5°C. Seventy-five naiads were handpicked and examined for eggs in the marsupia. Twenty gravid females were selected for the experimental infections. Embryos were extracted from the marsupia with a syringe and examined at 30X magnification for maturity. All embryos examined were immature.

Water temperatures ranged from 9°C-13°C on successive days. Water depth was 1.5 m. Mature glochidia were not collected until May 16, 1975, 31 days after the original collection.

Sample sizes ranged from 10-75 with an average of 25. Naiads were collected until May 23 when spawning ceased. Gonidea angulata were frequently collected in the M. m. falcata beds. However, G. angulata females were not gravid at the time M. m. falcata females were collected.

Naiads containing mature glochidia were placed in 1000 ml of aerated and chilled dechlorinated water. Naiads kept at the river temperature required an average time of 3 hours to abort glochidia. Naiads acclimated to room temperature aborted glochidia in 30 minutes. Aborted glochidia were placed in a 4000 ml beaker and stirred. An airline was placed inside the beaker. The stirring and aeration kept the glochidia suspended.

Coho salmon, chinook salmon, and steelhead trout presmolts were infected by individually exposing them to 8,000, 16,000, 32,000, 64,000, 128,000, and 256,000 parasites for 3 hours. Exposure chambers were 475 ml paper cups. Each cup contained 250 ml of dechlorinated water and was stirred with air.

Glochidia concentrations were estimated by pipetting 0.1 ml from the 4000 ml beaker stock and counting the viable glochidia at 30X. Viable glochidia showed the characteristic "winking" and passed a current of water.

Glochidia with swollen adductor muscles were not included. Counting was repeated five times. The average was used as the number of viable glochidia per 0.1 ml. Multiples of this concentration equal to 8,000, 16,000, 32,000, 64,000, 128,000, and 256,000 were used for infection concentration. It was necessary to keep the glochidia in suspension when determining exposure concentrations.

Ten presmolts of each species were placed in separate exposure chambers. Air and fish movement kept the glochidia suspended. Glochidia settled to the bottom unless suspended and fish had less chance of randomly coming in contact with each glochidium.

Ten control presmolts of each species were subjected to the same handling treatments as the test fish, but were not exposed to the glochidia. Fish were watched constantly during the 3 hr exposures. After exposure, the groups of fish were placed in separate 4-liter styrofoam aquariums located in a constant temperature room. Aquaria were aerated and supplied with running dechlorinated water at 9^{o}C, the approximated stream temperature.

Procedures were similar for the smolt infection trials, with two exceptions: 1) The exposure chambers were 15 cm x 15 cm aerated plastic trays, 2) The coho and chinook test and control fish had clipped fins for exposure level identification and after exposure all the fish were placed in a single 80-liter aquarium. All fish were fed a ration of Oregon moist pellets twice daily.

Mortalities of smolts and presmolts were recorded after 48 hours at each exposure concentration. The criteria for death was cessation of opercular movements. All fish were preserved in 10% buffered Formalin. All remaining presmolts were killed at the end of 48 hours; smolts were killed at 672 hours. Fish were preserved in 10% buffered Formalin. Parasites were counted on the four gills of one side of each fish and the resulting number was doubled to obtain the total parasite load. Karna (1973) and Meyers (1975) reported little difference in glochidial numbers on the two pairs of gills from either side of an infected fish. Average parasite numbers from the presmolts and smolts were compared at each exposure level.

Four gills from one side of an uninfected coho, chinook, and steelhead smolt and presmolt were removed to test for numbers of parasites per gm and per cc at each exposure concentration. Gill wet weights were taken for each fish species and type. The gills were then placed in a calibrated burette filled with water to the 5 ml mark and the volume that the gills displaced recorded. The resulting weight and volume figures were doubled. Ten fish of each species and type were subjected to the procedure. Average parasite numbers from the smolts and presmolts examined previously were used to calculate the number of parasites per gm or cc of gill tissue at each exposure concentration.

Condition Factor Exposure

For the condition factor experiment, four glochidial monolayers were made from the 4000 ml stock beaker by pipetting into beakers half full of dechlorinated water until a uniform glochidial layer settled on the bottom. Monolayers were stored in a refrigerator. Ten coho, chinook, and steelhead presmolts were selected for infection test fish. Test fish were individually separated and kept in compartments in aquaria with water running through each compartment. Ten fish of each species were used for controls and marked by removing fins. Fins removed were dorsal, left pectoral, right pectoral, anal, right pelvic, left pelvic, caudal, dorsal and anal, right pectoral and anal, and left pectoral and anal. Control fish of each species were kept together in one aquarium. Counts of viable glochidia were made daily for 5 successive days by placing the monolayered beaker on a mechanical stirrer and pipetting 0.1 ml onto a glass slide. The average of 5 counts was multiplied by ten to estimate the average number per ml.

Control and test fish were kept in separate 4-liter, aerated, styrofoam aquariums at 9°C. Each day for 10 days infection fish and controls were removed from their aquariums, weighed on a balance, and measured in a plastic runway before being subjected to glochidia. For 5 days ten fish from each species were infected by individually exposing them to 600 glochidia from the monolayers for 3 hours. Control fish were subjected to the same treatment but were not exposed to the glochidia. After exposure, fish were removed from the cups and returned to the aquarium. All fish were fed twice daily with ground Oregon Moist Pellets.

Parasite numbers were estimated by counting glochidia on the four gills of one side of each fish. The resulting number was doubled and recorded. Lengths and weights were recorded each day and daily condition factors (CF) calculated for each fish. The formula:

$$CF = (LC) \times (\text{wt. in gm})$$

was used where LC is tabulated length constant for a species, Carlander (1969). Graphs were drawn for each species to show the 10 day condition factor trend in test and control fish.

Margaritifera m. falcata Hosts

Native fishes were collected by electroshocking in the Willamette River at the collection site in May, 1975. Species and numbers of collected fishes were:
14 *Rhinichthys cataractae*, 19 *Richardsonius balteatus*, 3 *Oncorhynchus tshawytscha*, 4 *Cottus rhotheus*, 10 *Cottus asper*, and 3 *Cyprinus carpio*. All fish gills were

microscopically examined for glochidia at 30X diameters. Glochidia numbers were counted and recorded.

Water levels in the Willamette River were high and fish were seined from the Marys River, Oregon, at Bellfountain Road bridge, 4.8 km S.E. of Philomath. Fish were taken prior to spawning of M. m. falcata and the fish were probably free of any natural glochidia infections. Seven R. balteatus, six C. rhotheus, two C. perplexus, and six Rhinichthys osculus nubium were collected. Fish were placed in a 12-liter aquarium. Each fish was placed in 250 ml of aerated dechlorinated water and exposed to 2000 glochidia for 2 hours. Two coho smolts that were not exposed to the glochidia in the previous experiments were used as controls to test the viability of glochidia. After exposure, all fish were returned to the 12-liter aquarium and held 1 week. Fish were killed and examined for glochidia. Glochidial numbers were counted and recorded.

Artificial Spawning

In October 1976, 83 naiads were collected at the collection site. The naiads were brought to the laboratory at Oregon State University and placed in a 61 cm x 122 cm x 15 cm plastic tray with a water inlet from a 12-liter reservoir tank. A water outlet was located at the opposite end from the inlet. Water temperature was regulated at 4°C.

An algal culture of *Ankistrodesmus* provided nutrients for the naiads. A formulated media, (Hughes, Gorham, and Zehuder, 1958), provided nutrients for the algal culture. The naiads were fed 15 liters of culture. The culture was added to the reservoir tank and circulated through the plastic tray. The conditioning method of Loosanoff and Davis (1950) was used in an attempt to spawn *M. m. falcata* in the laboratory. Conditioning began in February, 1976.

RESULTS

Smolt and Presmolt Susceptibilities

Differences in the estimates of mean smolt and mean presmolt parasite number were calculated (Tables 1-3). Coho smolts were more susceptible to the glochidia than the coho presmolts at all concentration levels at the 0.05 level of probability (Table 1). Chinook smolts were less susceptible to the glochidia than the chinook presmolts at all concentration levels except 256,000 (Table 2). Steelhead smolts were more susceptible to the glochidia than the steelhead presmolts at all concentration levels (Table 3).

The results of experiments to determine the comparative resistance to glochidial infection between smolts and presmolts of each species are shown in Tables 4-9. Chinook smolts were more susceptible to the glochidia than coho smolts at all concentration levels (Table 4). Steelhead smolts were more susceptible to the glochidia than coho smolts at all concentration levels except 128,000 when tested at .05 level (Table 5). Chinook smolts were more susceptible to glochidia infections than the steelhead smolts at concentrations of 8,000, 16,000, and 32,000 parasites but less susceptible at concentrations of 64,000, 128,000, and 256,000 parasites (Table 6). Chinook presmolts were more susceptible to the glochidia

Table 1. Comparison between coho smolts and presmolts to glochidial infections of M. m. falcata based on the mean number of glochidia found on the gills.

Degrees of Freedom	Challenge Concentration	Mean Glochidia No. in Smolt	Mean Glochidia No. in Presmolt	t Value 0.05	Table t
18	8,000	575	82	7.2*	1.734
18	16,000	825	180	42.0**	1.734
18	32,000	1,256	421	14.0**	1.734
18	64,000	2,409	1,757	1.9*	1.734
18	128,000	4,269	3,080	6.6*	1.734
18	256,000	5,649	3,883	11.0**	1.734

Table 2. Comparison between chinook smolts and presmolts to glochidial infections of M. m. falcata based on the mean number of glochidia found on the gills.

Degrees of Freedom	Challenge Concentration	Mean Glochidia No. in Smolt	Mean Glochidia No. in Presmolt	t Value 0.05	Table t
18	8,000	1,406	2,098	-4.0*	1.734
18	16,000	1,840	2,497	-3.9*	1.734
18	32,000	2,433	3,411	-5.4*	1.734
18	64,000	3,108	4,762	-17.4**	1.734
18	128,000	5,221	6,847	-8.1*	1.734
18	256,000	8,553	8,077	-1.3	1.734

* Significant at 0.05 P.
** Significant at 0.01 P.

Table 3. Comparison between steelhead smolts and presmolts to glochidial infections of *M. m. falcata* based on the mean number of glochidia found on the gills.

Degrees of Freedom	Challenge Concentration	Mean Glochidia No. in Smolt	Mean Glochidia No. in Presmolt	t Value 0.05	Table t
18	8,000	2,433	178	32.0**	1.734
18	16,000	3,007	254	84.0**	1.734
18	32,000	3,060	551	47.6**	1.734
18	64,000	3,097	830	23.4**	1.734
18	128,000	4,558	1,327	36.2**	1.734
18	256,000	7,975	1,408	31.6**	1.734

Table 4. Comparison between coho smolts and chinook smolts to glochidial infections of *M. m. falcata* based on the mean number of glochidia found on the gills.

Degrees of Freedom	Challenge Concentration	Mean Glochidia No. in Chinook	Mean Glochidia No. in Coho	t Value 0.05	Table t
18	8,000	1,406	575	4.6*	1.734
18	16,000	1,840	825	6.1*	1.734
18	32,000	2,433	1,256	6.2*	1.734
18	64,000	3,108	2,409	5.0*	1.734
18	128,000	5,221	4,269	3.8*	1.734
18	256,000	8,553	5,649	7.2*	1.734

* Significant at 0.05 P.
** Significant at 0.01 P.

Table 5. Comparison between coho smolts and steelhead smolts to glochidial infections of M. m. falcata based on the mean number of glochidia found on the gills.

Degrees of Freedom	Challenge Concentration	Mean Glochidia No. in Steelhead	Mean Glochidia No. in Coho	t Value 0.05	Table t
18	8,000	2,433	575	19.3**	1.734
18	16,000	3,007	825	65.2**	1.734
18	32,000	3,060	1,256	23.0**	1.734
18	64,000	3,097	2,409	5.8*	1.734
18	128,000	4,558	4,269	1.6	1.734
18	256,000	7,975	5,649	9.0*	1.734

Table 6. Comparison between chinook smolts and steelhead smolts to glochidial infections of M. m. falcata based on the mean number of glochidia found on the gills.

Degrees of Freedom	Challenge Concentration	Mean Glochidia No. in Chinook	Mean Glochidia No. in Steelhead	t Value 0.05	Table t
18	8,000	2,433	1,406	2.5*	1.734
18	16,000	3,007	1,840	6.9*	1.734
18	32,000	3,060	2,433	3.3*	1.734
18	64,000	3,097	3,108	-0.8	1.734
18	128,000	4,558	5,221	-3.0*	1.734
18	256,000	7,975	8,553	-0.6	1.734

* Significant at 0.05 P.
** Significant at 0.01 P.

Table 7. Comparison between coho and chinook presmolts to glochidial infections of *M. m. falcata* based on the mean number of glochidia found on the gills.

Degrees of Freedom	Challenge Concentration	Mean Glochidia No. in Chinook	Mean Glochidia No. in Coho	t Value 0.05	Table t
18	8,000	2,098	82	77.5**	1.734
18	16,000	2,497	180	79.6**	1.734
18	32,000	3,411	421	90.8**	1.734
18	64,000	4,762	1,257	28.5**	1.734
18	128,000	6,847	3,080	36.9**	1.734
18	256,000	8,077	3,883	43.5**	1.734

Table 8. Comparison between coho and steelhead presmolts to glochidial infections of *M. m. falcata* based on the mean number of glochidia found on the gills.

Degrees of Freedom	Challenge Concentration	Mean Glochidia No. in Steelhead	Mean Glochidia No. in Coho	t Value 0.05	Table t
18	8,000	178	82	4.4*	1.734
18	16,000	254	180	5.9*	1.734
18	32,000	551	421	7.9*	1.734
18	64,000	830	1,257	-9.1*	1.734
18	128,000	1,327	3,080	-17.2**	1.734
18	256,000	1,408	3,883	-30.9**	1.734

* Significant at 0.05 P.
** Significant at 0.01 P.

Table 9. Comparison between chinook and steelhead presmolts to glochidial infections of *M. m. falcata* based on the mean number of glochidia found on the gills.

Degrees of Freedom	Challenge Concentration	Mean Glochidia No. in Chinook	Mean Glochidia No. in Steelhead	t Value 0.05	Table t
18	8,000	2,098	178	80.9**	1.734
18	16,000	2,497	254	73.1**	1.734
18	32,000	3,411	551	83.1**	1.734
18	64,000	4,762	830	114.8**	1.734
18	128,000	6,847	1,327	210.6**	1.734
18	256,000	8,077	1,408	250.4**	1.734

** Highly significant at 0.01 P.

than coho and steelhead presmolts at all concentration levels when tested at the .01 level (Tables 7 and 9). Steelhead presmolts were more susceptible than coho presmolts at concentrations of 8,000, 16,000, and 32,000 parasites but less susceptible at concentrations of 64,000, 128,000, and 256,000 parasites (Table 8). The chinook presmolt results agreed with Meyers' (1975) findings that chinook presmolts were more susceptible to glochidial infections than the coho presmolts (Table 9). Glochidia were encysted on all parts of the gill filaments in smolts and presmolts of each fish species.

The impact of glochidial infections on fish is more meaningful when the numbers of parasites/cc of gill tissue or the numbers of parasites/gm of gill tissue are plotted against exposure concentrations (Fig. 1-6). Damage to gill tissue from the parasite load can be estimated from the number of parasites per unit area but the area of gill tissue is not easily obtained. The number of parasites per unit of volume or weight probably is a meaningful measure of the effects of parasitism and provides a basis for comparing gill damage in fish of different sizes.

The numbers of parasites/cc of gill tissue and the numbers of parasites/gm of gill tissue were plotted against exposure concentrations for smolts and presmolts in Fig. 1-6. Glochidial numbers increased at each exposure concentration for all species.

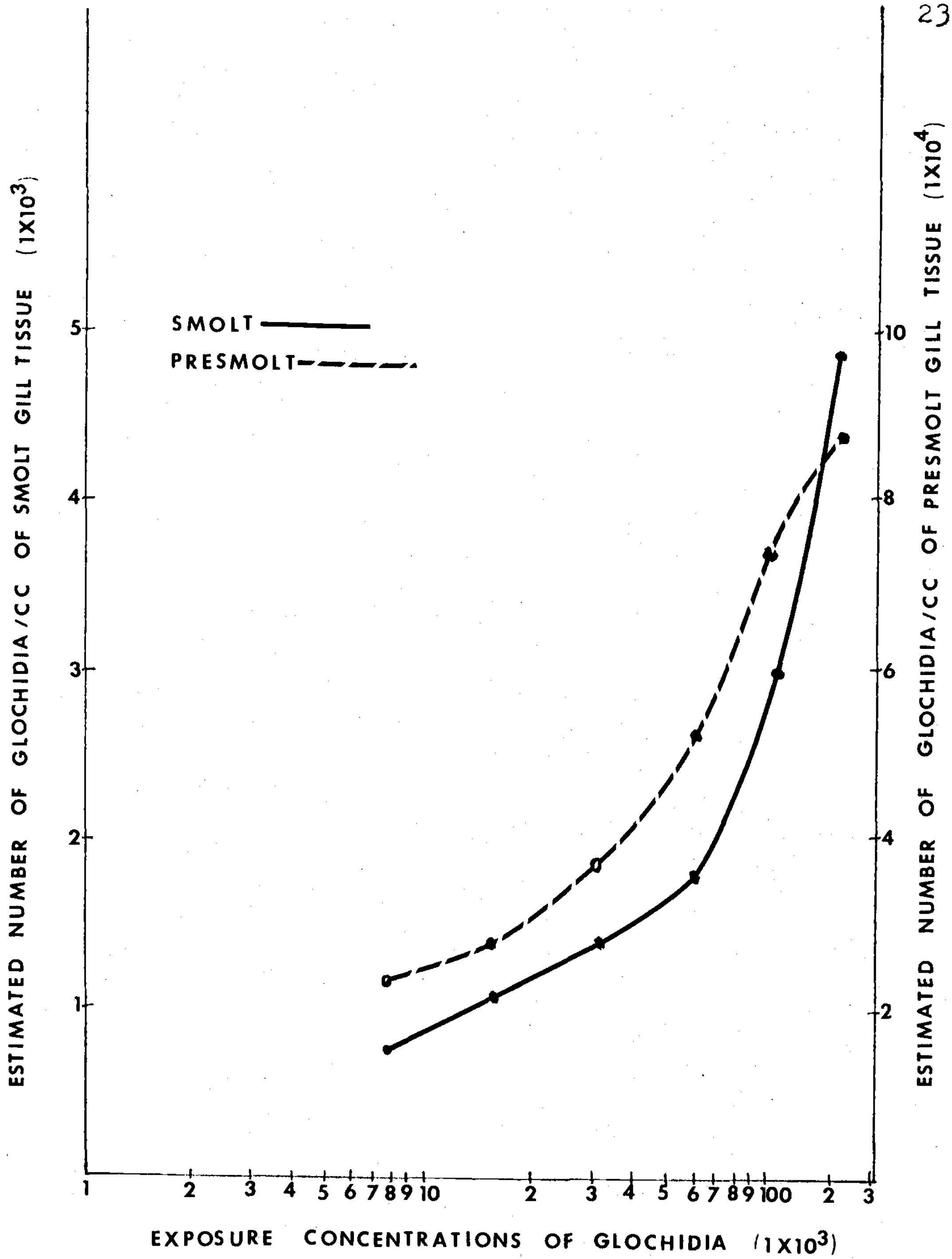

Figure 1. The estimated number of *M. m. falcata* glochidia per cc of chinook smolt and presmolt gill tissue at each exposure concentration.

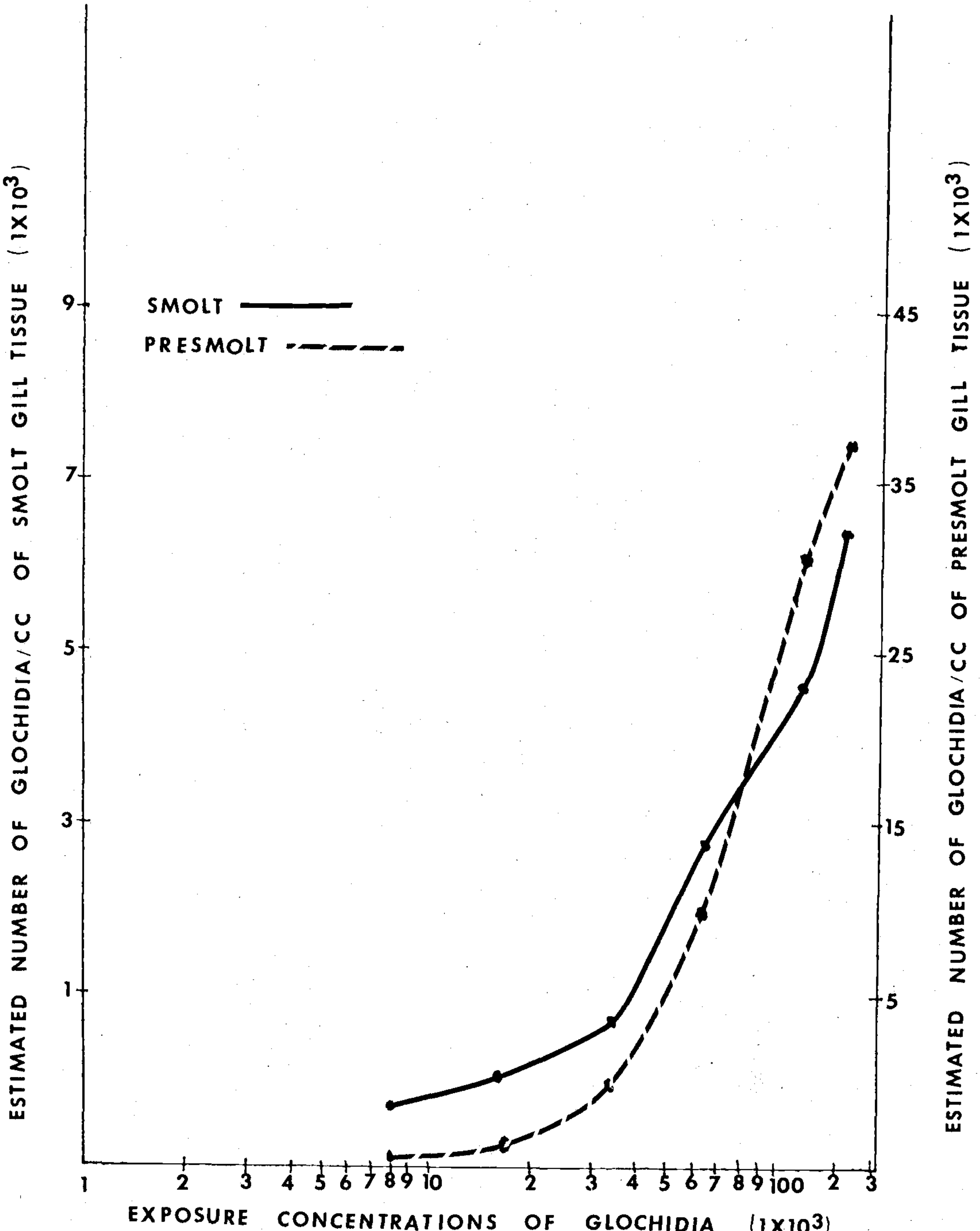

Figure 2. The estimated number of M. m. falcata glochidia per cc of coho smolt and presmolt gill tissue at each exposure concentration.

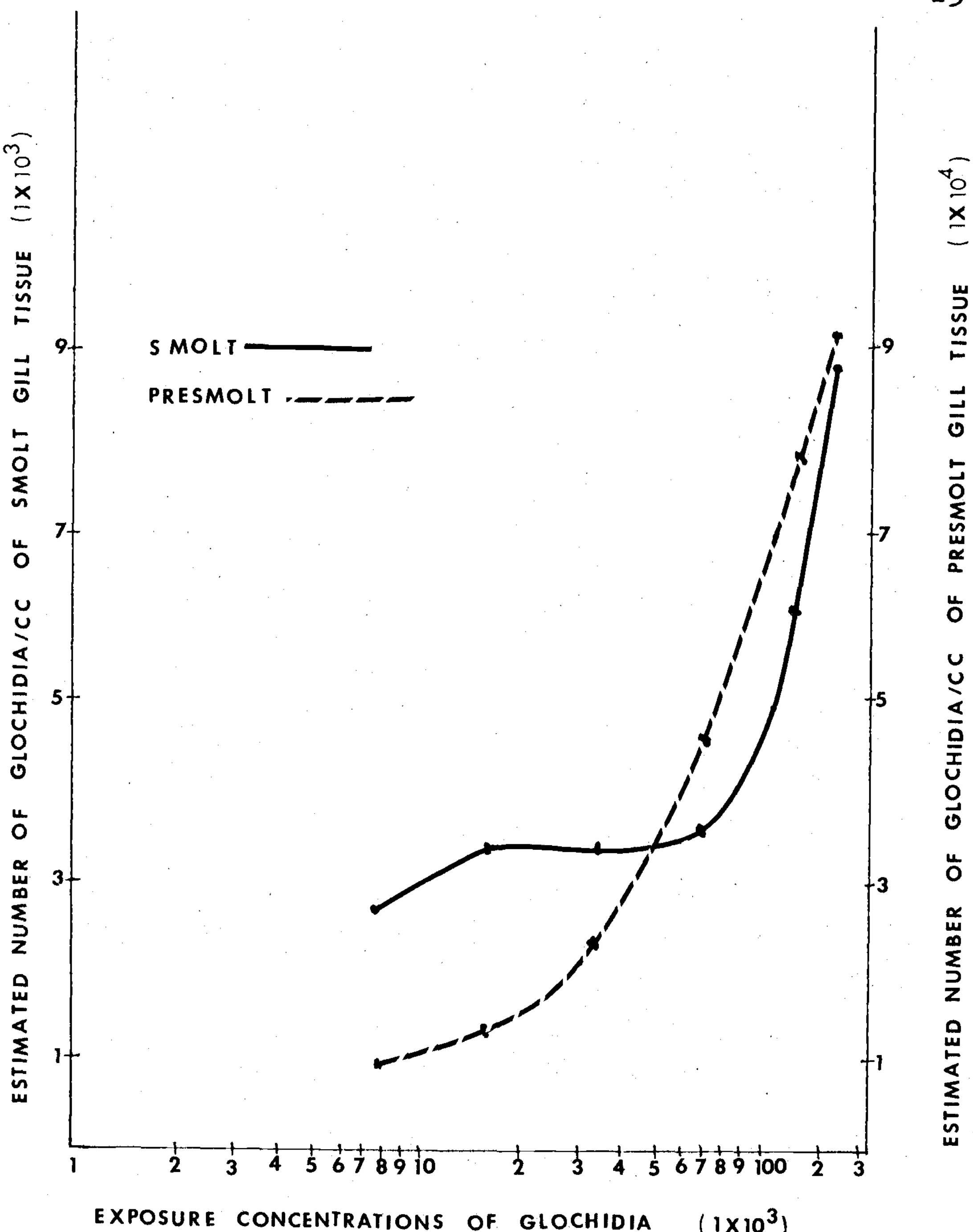

Figure 3. The estimated number of M. m. <u>falcata</u> glochidia per cc of steelhead <u>smolt</u> and presmolt gill tissue at each exposure concentration.

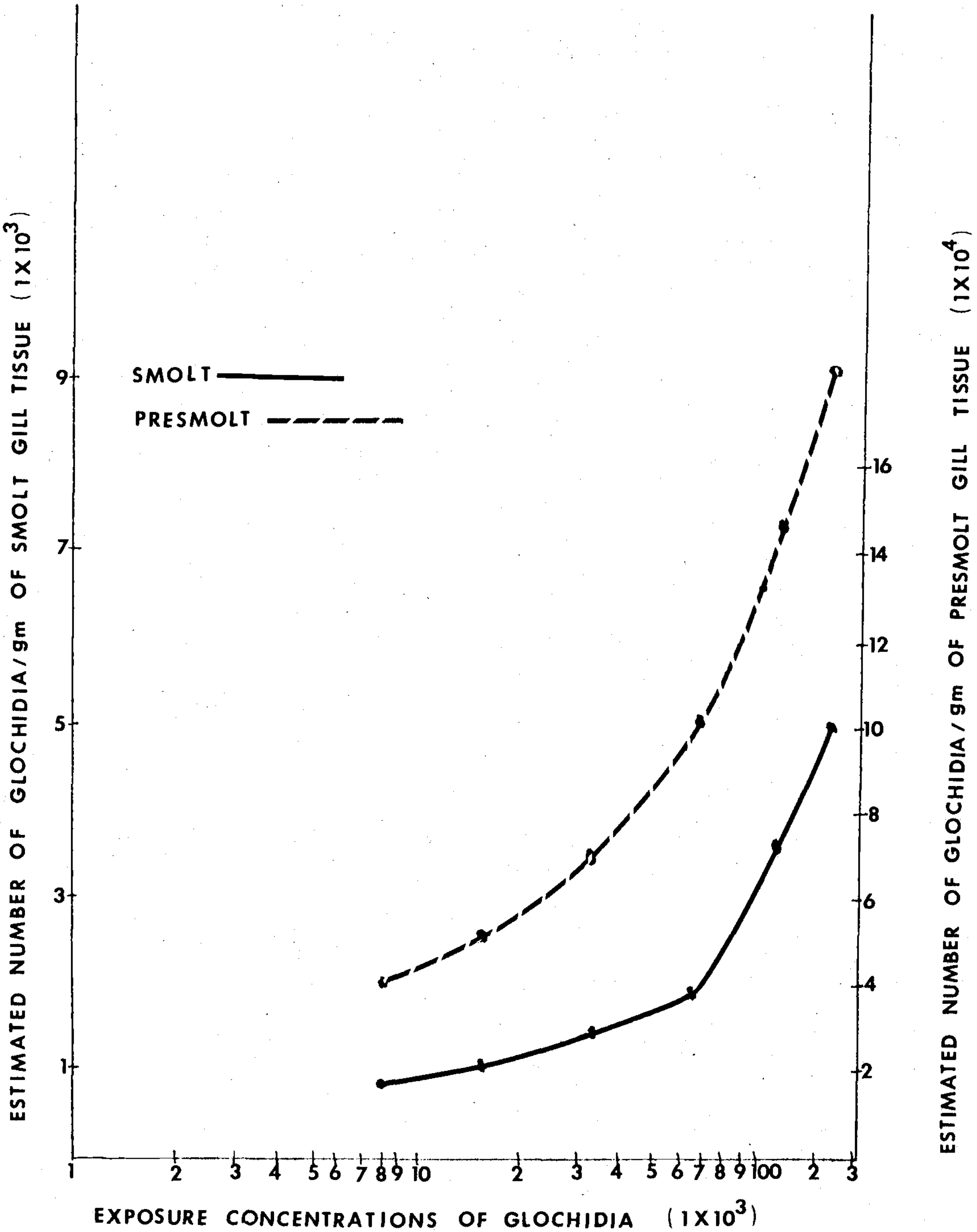

Figure 4. The estimated number of *M. m. falcata* glochidia per gm of chinook smolt and presmolt gill tissue at each exposure concentration.

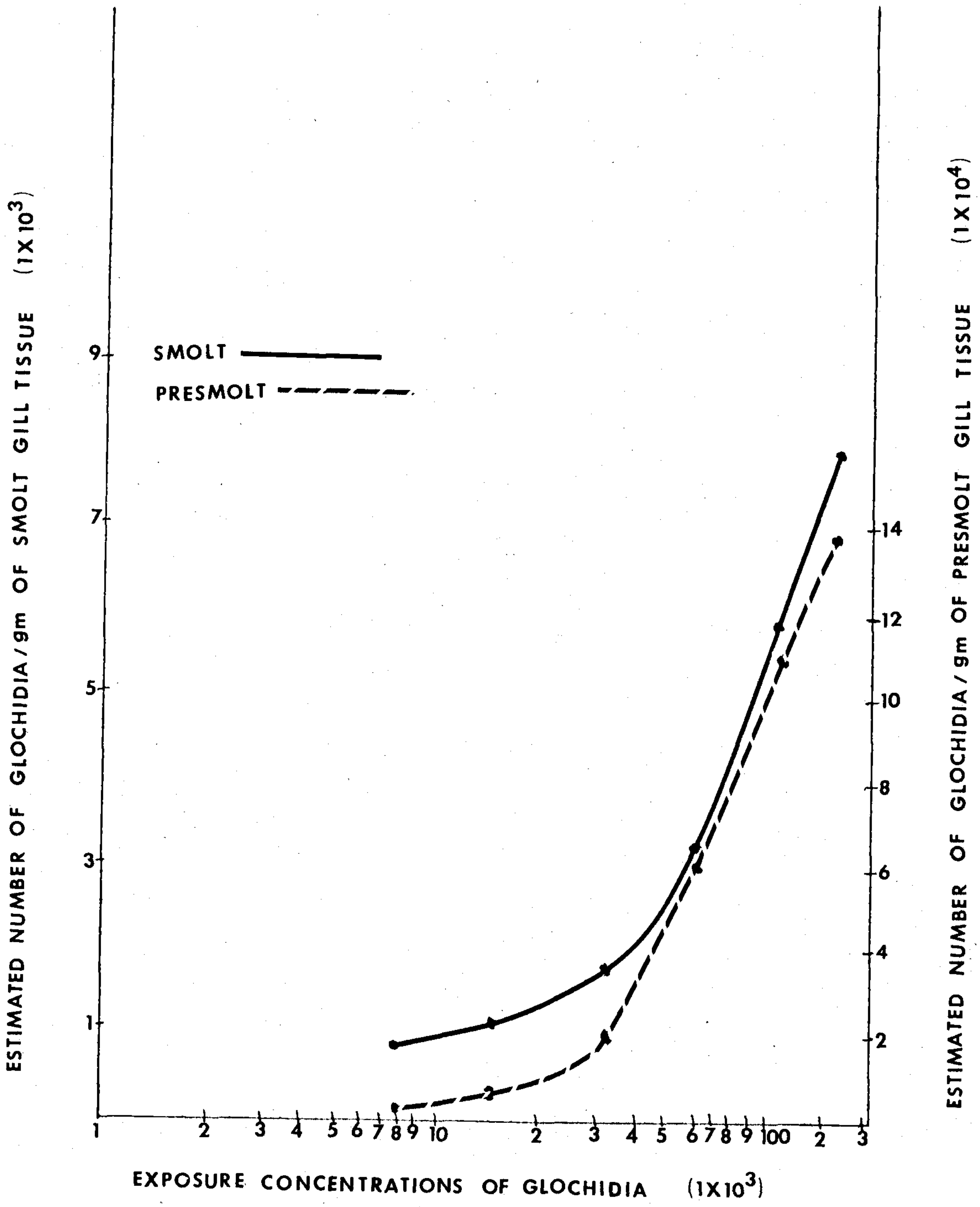

Figure 5. The estimated number of M. m. falcata glochidia per gm of coho smolt and presmolt gill tissue at each exposure concentration.

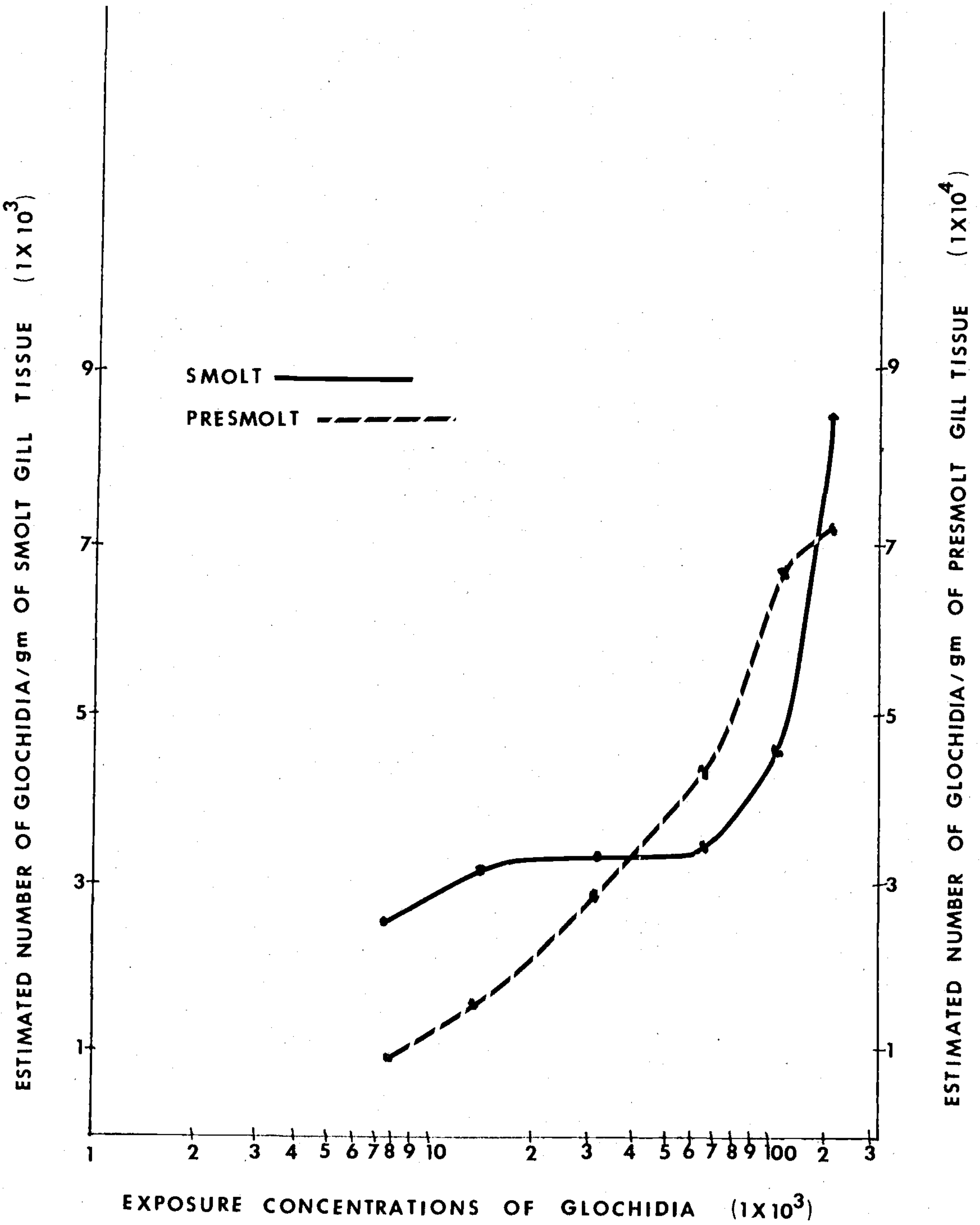

Figure 6. The estimated number of M. m. <u>falcata</u> glochidia per gm of steelhead <u>smolt</u> and presmolt gill tissue at each exposure concentration.

Condition Factor Exposures

Chinook, coho, and steelhead test fish showed a decline in condition factor (C.F.) or remained the same after 10 days of exposure (Figures 7, 9, 12). The C.F. of chinook, coho, and steelhead control fish remained the same, increased or decreased (Figures 8, 10, 11). One control fish died; a coho salmon with a probable Saprolegnia infection. Death among exposed fish amounted to 26%. Five chinook, and three coho test fish died. No steelhead test fish died. Mean parasite numbers in test fish were: 716 in chinook, 547 in coho, and 199 in steelhead. The parasite number ranged from 211-1137 in chinook, 154-813 in coho, and 31-388 in steelhead test fish. The C.F. of two chinook test fish remained constant throughout the 10 day experiment. Five chinook test fish died and three showed C.F. declines. The five dead fish had decreases in C.F. before death (Appendix). The C.F. of seven coho test fish declined and three fish died. Two fish showed C.F. decreases before death and one remained the same before death (Appendix). The C.F. of one steelhead test fish remained the same but the other nine fish showed C.F. declines (Appendix).

The C.F. of four chinook control fish remained the same while one showed an increase and five a decrease (Appendix). Three coho control fish had condition factors that remained the same during the experiment, one died from a fungus Saprolegnia, and six showed an increase (Appendix). Seven steelhead showed C.F. increases, one a decrease, and two remained the same (Appendix).

Linear regressions were plotted for each species, (Figures 13-15), and the r values calculated. The r value of the coho salmon was 0.9484. The r value of the chinook salmon was 0.9216 and the r value of the steelhead trout was 0.9000.

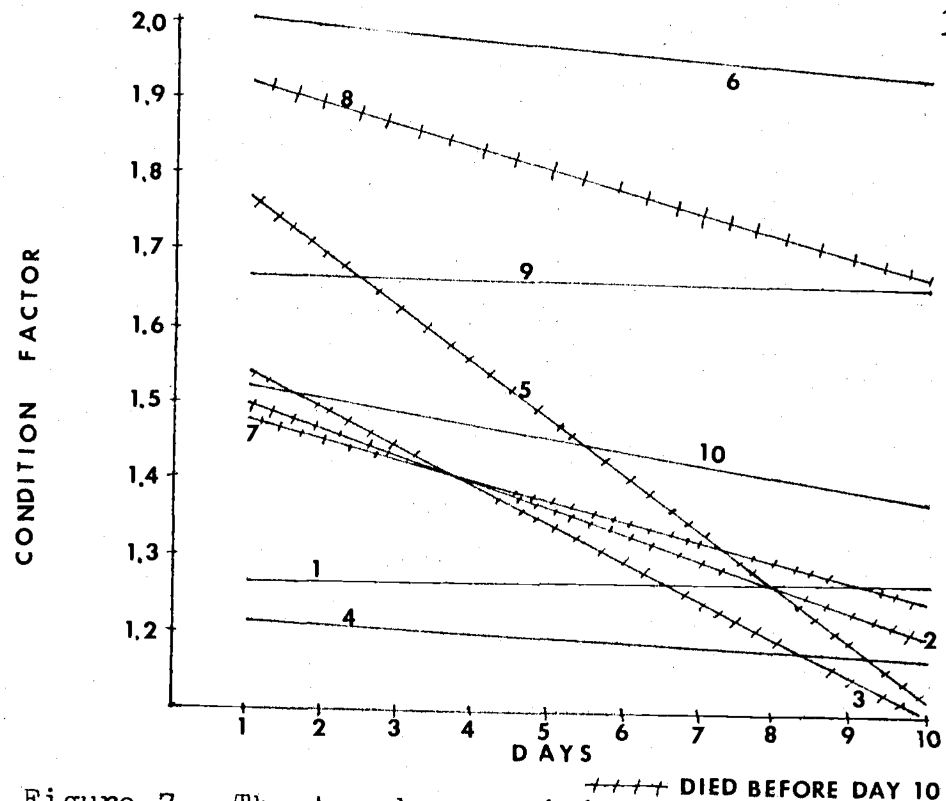

Figure 7. The ten day condition factor of ten chinook test fish exposed to the glochidia of M. m. falcata.

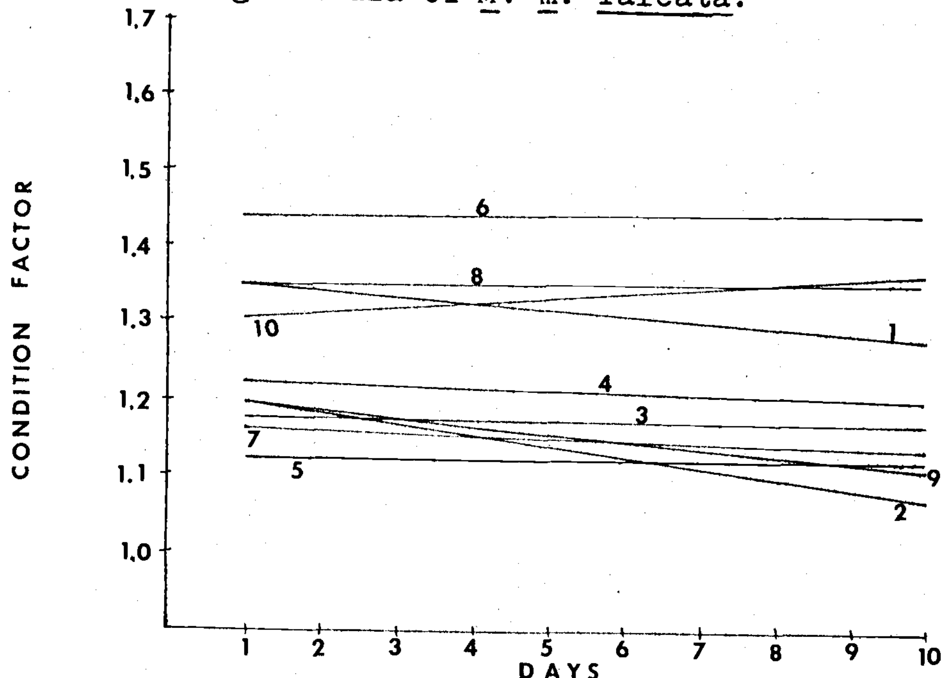

Figure 8. The ten day condition factors of ten chinook control fish not exposed to the glochidia of M. m. falcata.

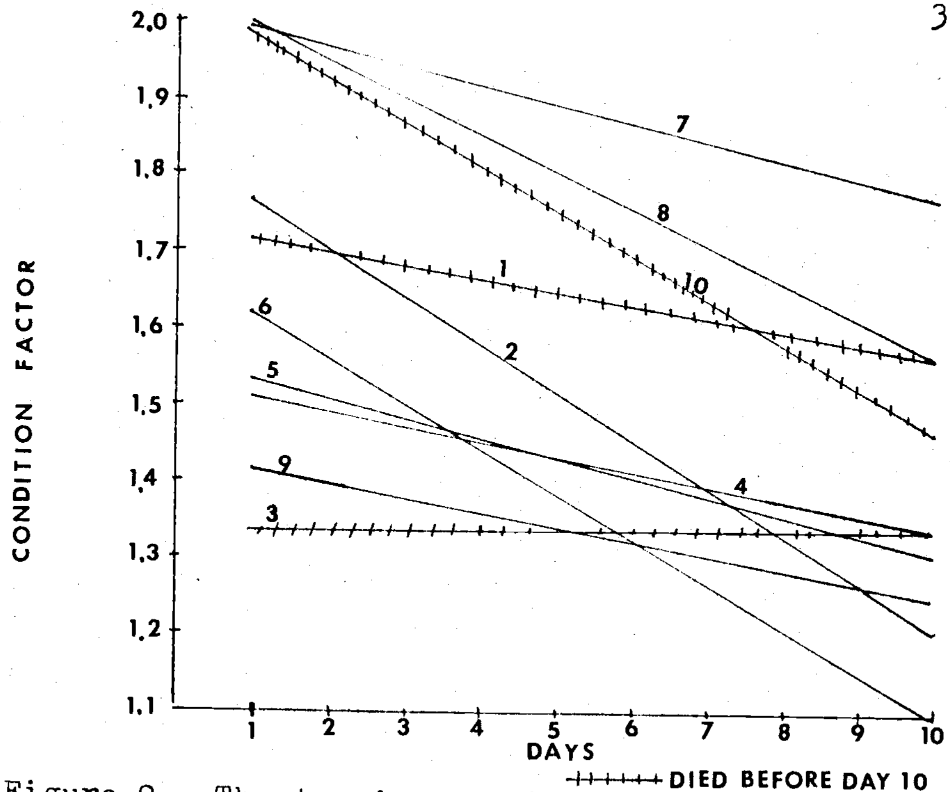

Figure 9. The ten day condition factors of ten coho test fish exposed to the glochidia of M. m. falcata.

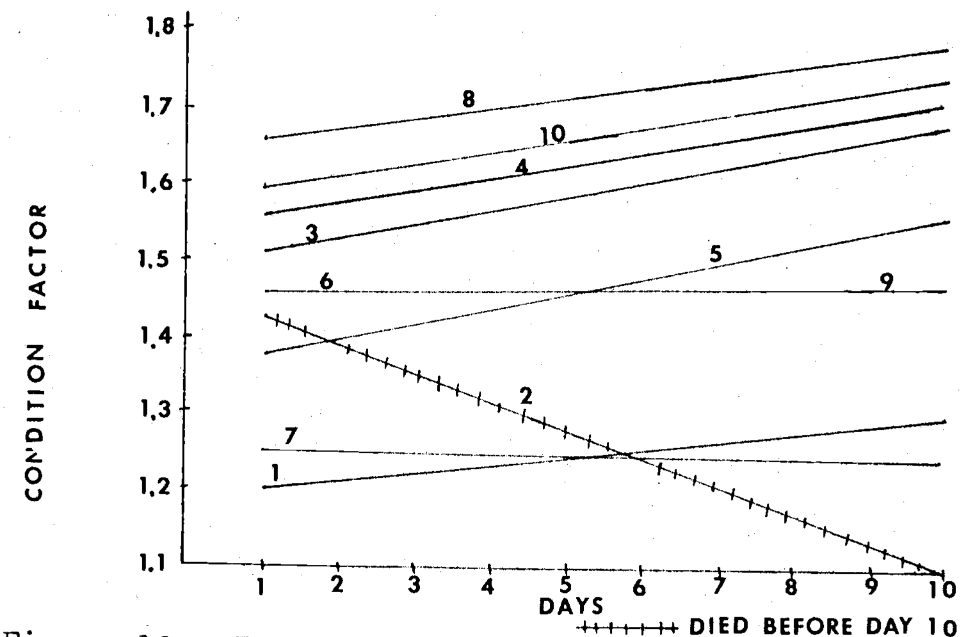

Figure 10. The ten day condition factors of ten coho control fish not exposed to the glochidia of M. m. falcata.

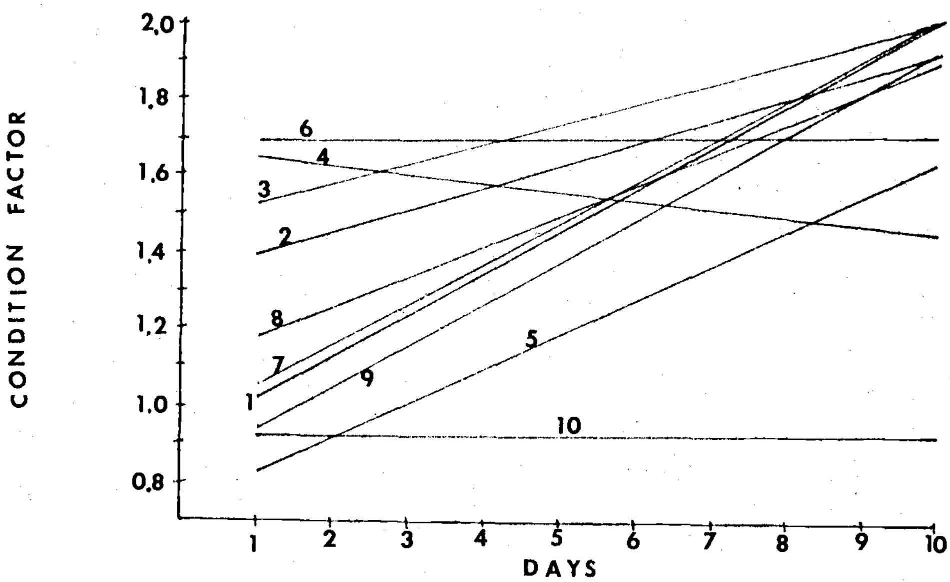

Figure 11. The ten day condition factors of ten steelhead control fish not exposed to the glochidia of M. m. falcata.

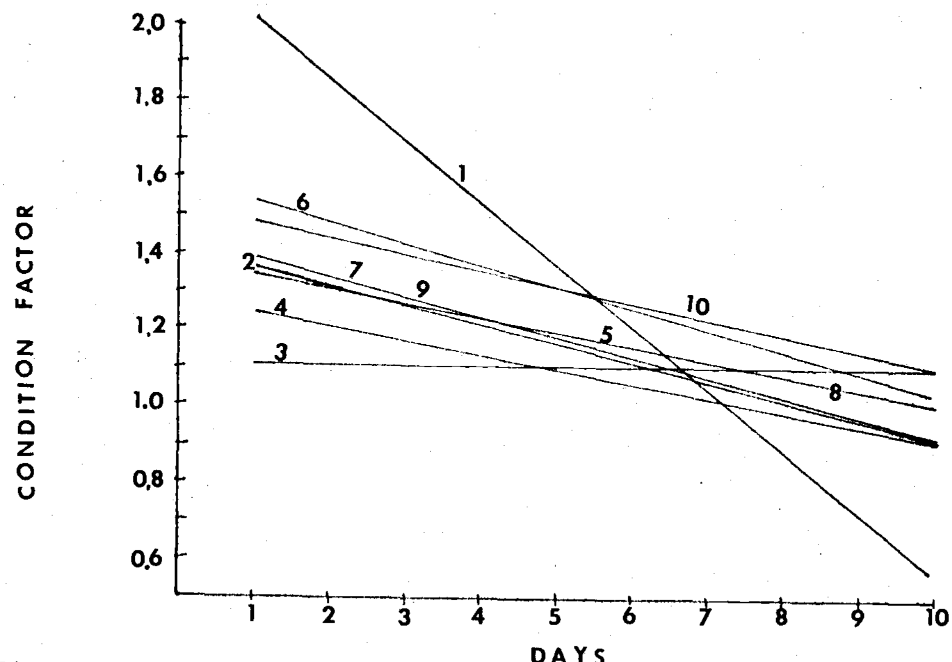

Figure 12. The ten day condition factors of ten steelhead test fish exposed to the glochidia of M. m. falcata.

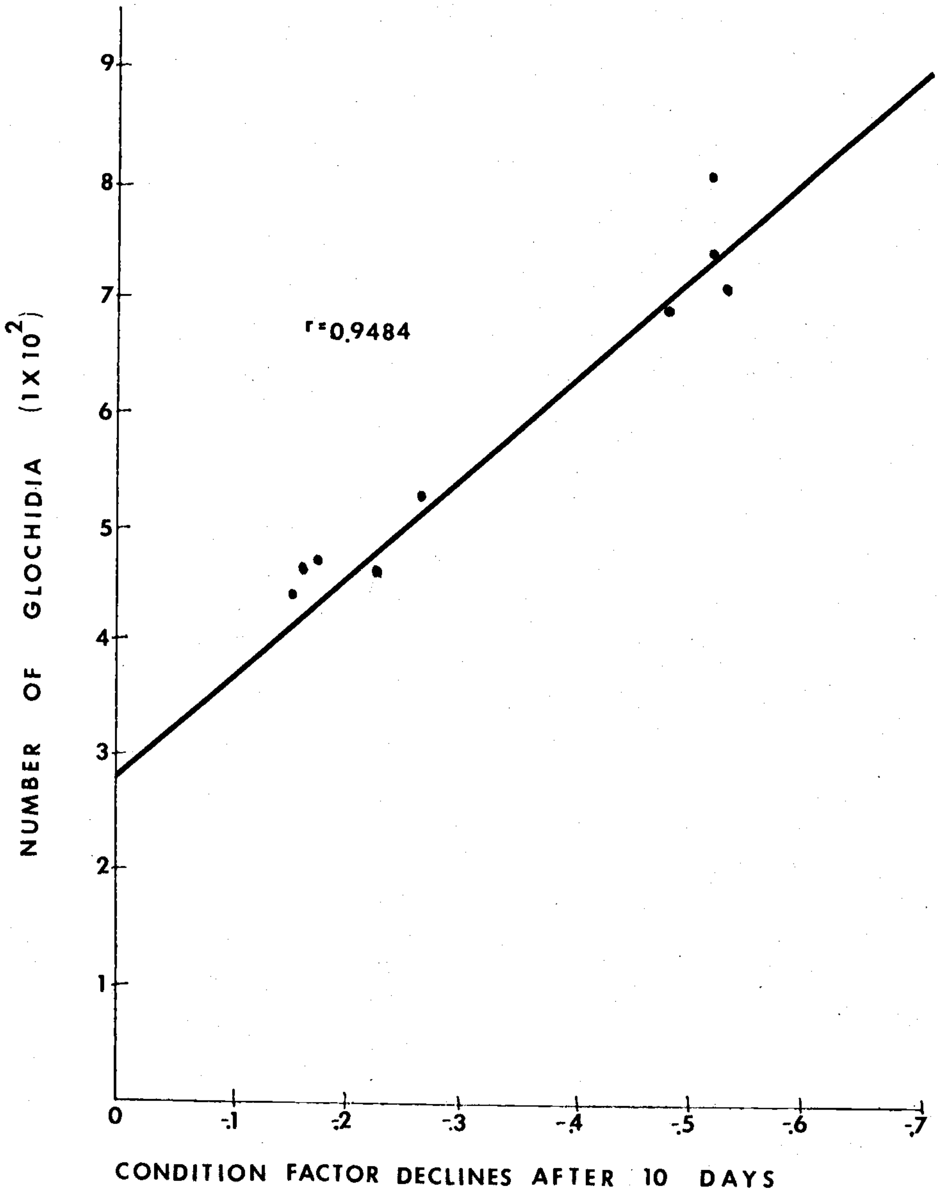

Figure 13. Regression of the condition factor of coho versus the number of glochidia after 10 days exposure.

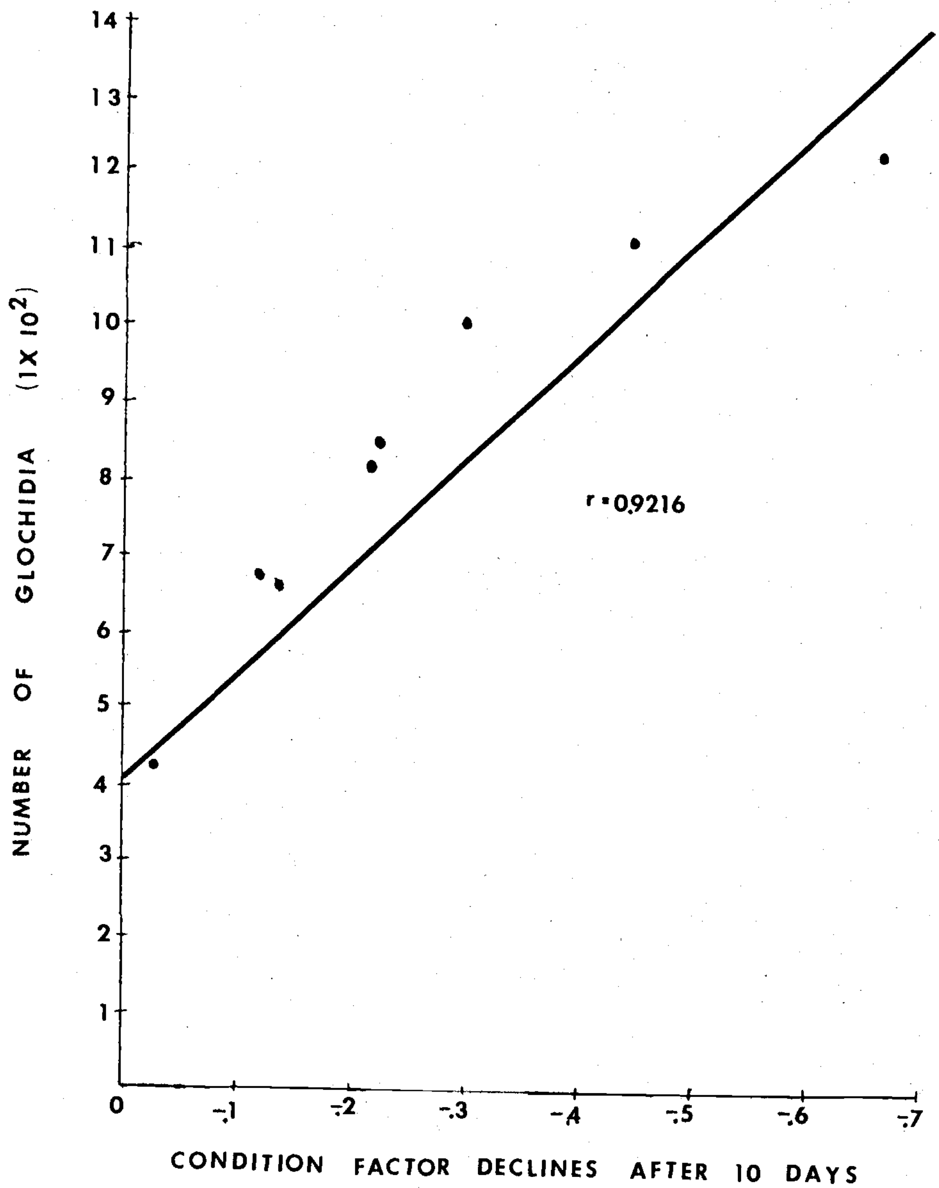

Figure 14. Regression of the condition factor of chinook versus the number of glochidia after 10 days exposure.

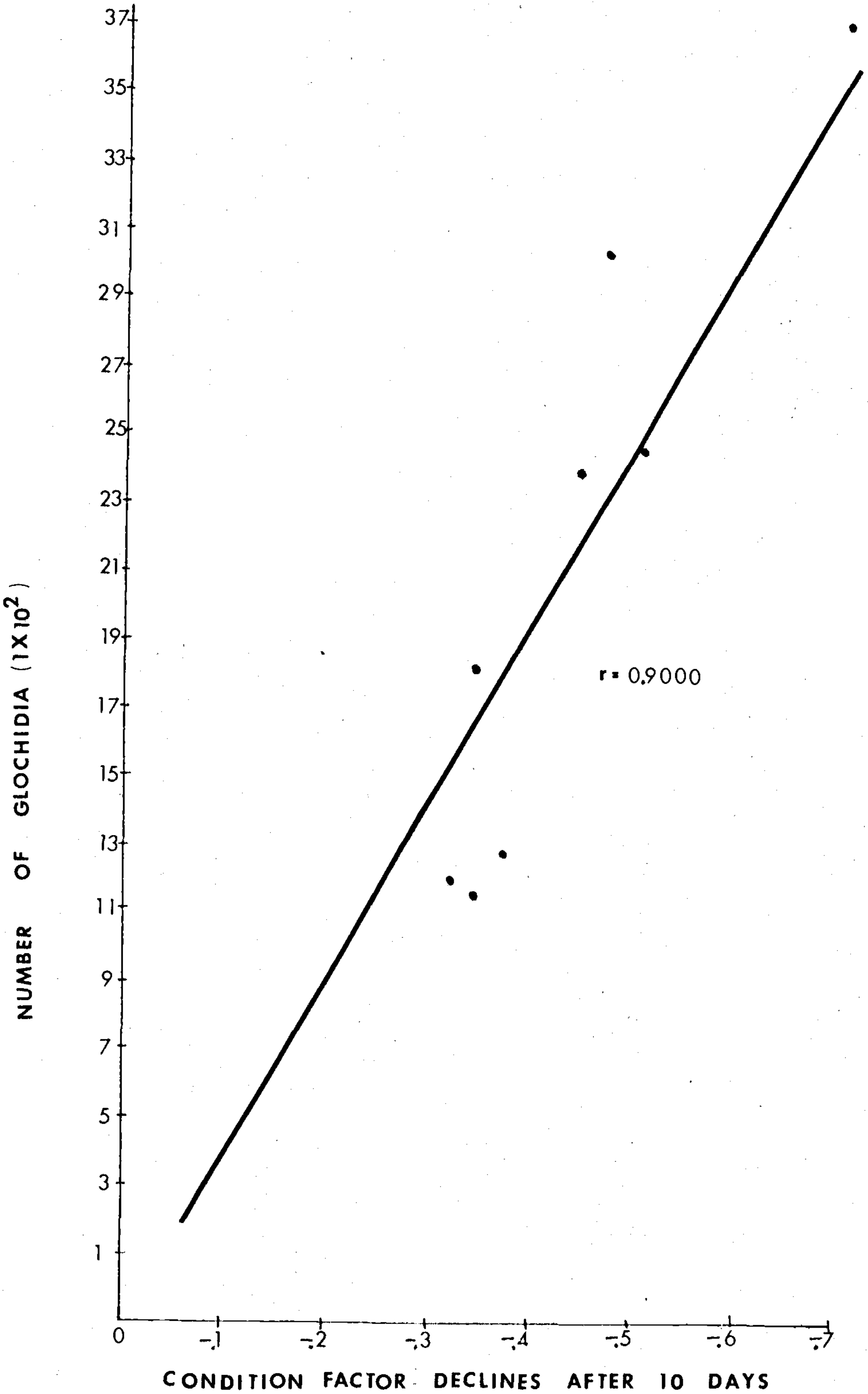

Figure 15. Regression of the condition factor of steelhead versus the number of glochidia after 10 days exposure.

Margaritifera m. falcata Hosts

Four species of Willamette River fish, chinook salmon, longnose dace, torrent sculpin, and prickly sculpin contained encysted glochidia (Table 10). The average numbers of attached glochidia were: chinook salmon 17; longnose dace 7; torrent sculpin 4; and prickly sculpin 5. Glochidia were encysted on all parts of the gill filaments. Glochidia were not present on carp, redside shiners, and largescale suckers.

The torrent sculpin and coho smolt were the only fish artificially infected with encysted glochidia (Table 11). The torrent sculpin had an average glochidial number of 31 with a range of 4-46. Glochidia did not infect redside shiners, blackside dace, or reticulate sculpins. Viability of the glochidia was measured by subjecting two unexposed coho to glochidia. The coho were used as control fish in previous experiments. The two coho developed parasitic numbers of 243 and 116 respectively indicating the viability of the glochidia. No artificially infected fish died during or after exposure to glochidia.

Glochidia on the native fish collected were *M. m. falcata*. Only two other naiads are present in the Willamette River, *Anodonta* sp. and *G. angulata*. The glochidia of *Anodonta* sp. are ectoparasites (Wood, 1973; Ingram, 1948) and no glochidia were encysted on the fins.

Table 10. Number of glochidia attached to collected native fish infected with *M. m. falcata* glochidia.

Species	No. Fish Examined	No. Fish Infected	Total No. Parasites
Rhinichthys cataractae	14	14	104
Catostomus macrocheilus	9	0	0
Oncorhynchus tshawytscha	3	3	52
Cyprinus carpio	3	0	0
Cottus rhotheus	4	4	18
Richardsonius balteatus	19	0	0
Cottus asper	10	9	50

Table 11. Number of glochidia attached to fish artificially infected with *M. m. falcata* glochidia.

Species	No. Fish Examined	No. Fish Infected	Total No. Parasites
Richardsonius balteatus	7	0	0
Cottus perplexus	2	0	0
Rhinichthys osculus nubilus	6	0	0
Cottus rhotheus	6	6	186
Oncorhynchus kisutch	2	2	359

G. angulata populations spawn at a time later than *M. m. falcata*

Artificial Spawning

After conditioning for 2 weeks at an average temperature of 13°C, the gonads of three male naiads had sperm and seven females had eggs when a sample was taken by syringe. After 3 weeks all 83 naiads contained either eggs or sperm. The river naiads examined at the same time did not have eggs or sperm present in the gonads. However, there was no spawning of males or females 4 weeks after the original conditioning period. Water temperatures were manipulated to force the naiads into spawning, but this was not successful. Sperm suspensions from male naiads were placed in the water to encourage the release of eggs and sperm. This was also unsuccessful.

Loosenoff and Davis (1963) were successful in inducing spawning by stretching the adductor muscles with pegs inserted between the shells. Pegs were inserted to stretch the adductor muscles but spawning of *M. m. falcata* did not occur. Male naiads spawned after feeding was increased from weekly to daily rations. This was 6 weeks after the original conditioning period. River naiads also had sperm present in their gonads at this time. The female naiads in captivity did not spawn nor were eggs passed from the gonads to the marsupia. Eight female naiads died during the experiment.

DISCUSSION

Chinook salmon were more susceptible to glochidial infection than coho and steelhead. However, susceptibility differences between coho and steelhead were less distinct. Meyers (1975) compared the relative susceptibility of chinook, steelhead, and coho presmolts to glochial infections of M. m. falcata and found chinook the species most susceptible followed by steelhead and coho. I found steelhead presmolts were more susceptible than coho to infections at challenge concentrations of 8,000, 16,000, and 32,000 glochidia (Table 8). However, at challenge concentrations of 64,000, 128,000, and 256,000 coho were more susceptible to infection than steelhead presmolts. There is no obvious explanation for the reversal in susceptibility between the two species. The "t" test indicated that the susceptibility difference was real and some probable explanations for the reversal in susceptibility need mentioning.

Comparisons of glochidial numbers in smolts and presmolts can only be made if space differences in the gills do not limit glochidial infections. The smolts have a much larger gill area and volume than presmolts and are capable of supporting a larger number of glochidia. Differences in space between the gill filaments of smolts and presmolts might cause differences in glochidial attachment on a mechanical basis. It was assumed in this study that glochidia which average 70 micro meters (μm) in length, 75 μm in height, and 40 μm in depth had an equal chance of attaching to the gills of a smolt or presmolt. Although spaces between lamella in filaments may be larger in smolts than in presmolts, 80 μm compared to 30 μm, the smolt gill filaments are longer than presmolt gill filaments, 3000 μm compared to 800 μm. Therefore, I assumed the glochidia had an equal chance of attaching to a smolt gill as a presmolt gill.

The possibility of space limiting infection was explored by plotting the number of glochidia/cc gill tissue against the log of concentrations for all smolt and presmolt infection tests (Figures 1-6). The number of glochidia/cc of gill tissue continued to increase as fish were subjected to higher exposure concentrations in all cases with the possible exception of steelhead at the 256,000 concentration. The rate of increase strongly suggested that space did not limit encystment of the glochidia on the gills. However, microscopic examination of the gills exposed to high concentrations of glochidia revealed little additional space was available for encystment in any of the presmolt's gills. Comparisons between the volume of glochidial space occupied and volume of the gills indicated that space might have been close to limiting infections. As glochidial exposure concentrations increased, the volume of attached glochidia/cc increased substantially, while the volume of the gills stretched but remained fairly constant. It became evident with the number of glochidia/cc reaching high numbers and only a finite amount of space available, that the number of glochidia the gills were able to accommodate probably was close to maximum. Microscopic examination showed some evidence of crowding. Importantly, doubling of glochidial exposure concentrations to presmolts did not cause a doubling in glochidial numbers attaching. For example, at the 128,000 exposure concentration, chinook, coho and steelhead have glochidial numbers of 6,847, 3,080, and 1,327, respectively. However, at the 256,000 exposure concentration, glochidial numbers only increased to 8,077, 3,883, and 1,408, representing gains of 16%, 21%, and 7%, respectively. Meyers (1975) found the same relationships with presmolt fishes he infected. This suggests that a physiological response of the fish or parasite may limit attachment numbers once a certain level of attachment has been established.

Additionally, glochidia increase 500% in size before excysting from the gills. Although the gill tissue "stretches" when glochidia attach, a heavy glochidial load combined with a 500% increase may cause crowding of the glochidia. A heavy glochidial loan may also cause severe clubbing of the gills. This may result in death to the fish by impeding osmoregulation and gas transfer across the gills and ultimately, death of the parasite. Severe clubbing of the gills was evident in all presmolts of this study at the higher glochidial exposure concentrations.

A physiological reaction may also have contributed to the reversals in glochidial numbers. Fustish (1976) found coho salmon mucus and blood was more lethal to glochidia than chinook mucus and blood. He also showed that coho slough glochidia more readily than chinook. However, no comparisons were made between these two species and steelhead trout. The steelhead presmolts may have sloughed glochidia more readily than the coho presmolts at the higher glochidial exposure concentrations. Chinook smolts may also be sloughing glochidia more readily than steelhead smolts at the higher exposure concentrations where another reversal in numbers occurred.

Factors covering surface area space limitations, maximum glochidial loads, and physiological reactions were examined to explain why steelhead and coho presmolt glochidial numbers reversed. The reason is probably due to a physiological reaction. Increases in attached glochidia indicate there was enough room for more parasites to attach on all fish species and no limiting mechanism was obvious (Fig. 1-6). Studies by Fustish (1976) show that physiological reactions can cause differences in glochidial numbers between fish species. The physiological reaction appears to be the most reasonable explanation for the shift in glochidial numbers between coho and steelhead presmolts, and chinook and steelhead smolts.

Comparison of glochidial infections can be supported on a quantitative basis but caution must be applied to comparisons at high exposure concentrations of glochidia. Comparisons are probably real at the lower concentrations but not at the higher concentrations.

The ability of M. m. falcata glochidia to infect smolts and presmolts readily indicates both fish sizes serve as hosts. Meyers (1975) showed that secondary fundal infections were detrimental to large numbers of presmolts infected with M. m. falcata glochidia. High numbers of encysting glochidia may enable secondary invaders; i.e., fungi and bacteria, to infect smolt gills. Secondary infections may increase the mortalities of smolts.

Naiads occur on gravel or sand substrate bottoms. In a river system, rocky substrates and rapid flowing headwaters are usually located upstream. As a river flows towards the ocean, sediment particles begin to settle out. The river bottom changes to gravel, sand, and, eventually, to silt. Naiads located far upstream usually have worn shells from the water and rock action. If the naiad had a mechanism for being transported downstream, new colonies could be established in favorable water and substrate conditions. The ability of the glochidia to infect smolts may have an evolutionary significance. By infecting smolts, the naiad could be moved to new downstream areas for habitation. Infection of presmolts or native fish would move naiad populations upstream or keep them stationary. The ability of naiads to be moved to new areas for habitation may explain the wide geographic distribution of M. m. falcata.

An increase in the condition factor can be used as a measurement of growth when growth is defined as the elaboration of tissue. Glochidia infections generally depressed condition factors in all species and infections have an apparent effect on growth. Condition factors declined in infected chinook, coho, and steelhead. Control fish showed increasing condition factors, maintained their condition factor, or had smaller declines in C.F. than test fish. Decline of C.F. and growth was directly attributed to glochidial infections. Control fish were handled as much as test fish and handling probably caused the few declines in condition factor. Handling was not entirely responsible for the condition factor decrease in test fish. No test fish showed a positive condition factor and declines were substantial: in one case up to 72%. Only test fish showed high declines in condition factor and glochidia attachment must have been the primary factor responsible for the decline. Fish have difficulty in tolerating high declines in condition factor, and declines in C.F. were found in all test fish that died. Regressions indicated there was a direct relationship between the number of glochidia attached to the gill of all species infected and C.F. declines (Fig. 13-15). Fish with high glochidial numbers showed a greater decline in C.F. than fish with low glochidial numbers.

Glochidia apparently interfered with metabolism. Migrating salmonids must be in excellent condition to survive the journey downstream and to make the osmotic adjustments required for life in salt water.

The wide distribution of *M. m. falcata* indicates a large number of fish probably serve as hosts. Trout have been observed to be naturally infected with *Margaritifera* glochidia (Wilson, 1916; Murphy, 1942). Experimental infection was established in brown trout, *Salmo trutta*, rainbow, *Salmo gairdneri*, and brook trout, *Salvelinus fontinalis*, (Murphy, 1942); and several kinds of minnows (Harms, 1907; Murphy, 1942).

Murphy (1942) was not able to induce artificial infection in the sculpin *Cottus bairdii beldingi*. Surber (1912) listed natural hosts of other freshwater naiads. In a search of other possible hosts, the torrent sculpin (*Cottus rhotheus*) was artificially infected with glochidia from *M. m. falcata*. The prickly sculpin and longnose dace also harbored glochidia. Artificial infection was not successful in the redside shiner, blackside dace, and reticulate sculpin. The torrent sculpin, prickly sculpin, and longnose dace make good hosts for M. m. falcata because the host-parasite relationship is environmentally related. All three fish species and M. m. falcata are found in swift flowing waters. Glochidia can attach to the torrent sculpin, longnose dace, and prickly sculpin and grow, excyst, and settle to the substrate bottom to continue their life cycle. The swift flowing water meets the necessary water requirement for bottom establishment. Ability of the naiad to infect native fish may move naiad populations upstream or keep them stationary. Excystment from other hosts might drop the young naiads in unsuitable habitat and halt the life cycle. More work must be done to establish other hosts for M. m. falcata.

Obtaining naiad gametes out of season would be useful. Currently, experimentation with M. m. falcata can only be done in spring during natural spawning. Obtaining gametes out of season would permit continuous experimentation.

Loosanoff (1937, 1942) showed that marine bivalves can be conditioned for late fall and early winter spawning only after recovery from the natural spawning activities of the preceding spring and summer. The recovery consists of complex physiological processes generally leading to accumulation of reserve materials, particularly glycogen.

The development of gametes is temperature dependent. Eggs and sperm of _M. m. falcata_ were obtained in the winter after a 2 week temperature conditioning period. This agreed with Loosanoff and Davis (1950) who stated that the optimal conditioning period for marine bivalves is 2-3 weeks.

Gametes were obtained from _M. m. falcata_ out of season and males spawned but female naiads did not spawn in the laboratory. Eggs were not passed from the gonad to the marsupia. An incomplete weekly ration probably resulted in a lack of sufficient energy. Female naiads probably would have spawned if fed more often. Male naiads spawned only after feeding was increased from weekly to daily rations. Female naiads probably used too much energy for egg formation and maintenance and did not have enough for egg passage and spawning. Deaths of eight female naiads probably were the result of improper diets. No females died after feeding was increased from weekly to daily. All other spawning methods--temperature shock, sperm suspensions, and stretched adductor muscles were unsuccessful.

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APPENDIX

Comparison of chinook test fish condition factors at day 1 and day 10 after exposure to the glochidia of _M. m. falcata_.

Fish No.	No. Parasites Attached	C.F. Day 1	C.F. Day 10	C.F. increase-decrease
1	211	1.27	1.27	0%
2	1,013	1.50	1.20*	-20%
3	1,077	1.54	1.10*	-29%
4	446	1.21	1.18	- 3%
5	1,137	1.78	1.13*	-36%
6	665	2.08	1.94	- 7%
7	819	1.48	1.25*	-16%
8	787	1.92	1.68*	-13%
9	329	1.67	1.67	0%
10	671	1.52	1.39	- 9%

* Died before day 10.

Comparison of coho test fish condition factors at day 1 and day 10 after exposure to the glochidia of _M. m. falcata_.

Fish No.	No. Parasites Attached	C.F. Day 1	C.F. Day 10	C.F. increase-decrease
1	438	1.71	1.56*	- 9%
2	693	1.75	1.20	-31%
3	154	1.34	1.34*	0%
4	491	1.51	1.34	-11%
5	452	1.53	1.31	-14%
6	757	1.62	1.08	-33%
7	512	2.01	1.76	-12%
8	672	2.03	1.56	-23%
9	486	1.41	1.25	-11%
10	813	2.00	1.46*	-27%

* Died before day 10

Comparison of steelhead test fish condition factors at day 1 and day 10 after exposure to the glochidia of *M. m. falcata*.

Fish No.	No. Parasites Attached	C.F. Day 1	C.F. Day 10	C.F. increase-decrease
1	388	2.28	0.59	-74%
2	239	1.36	0.91	-33%
3	31	1.11	1.11	0%
4	115	1.22	0.91	-25%
5	181	1.34	1.00	-25%
6	247	1.52	1.02	-33%
7	294	1.37	0.91	-34%
8	111	1.34	1.00	-25%
9	122	1.48	1.11	-34%
10	122	1.48	1.11	-25%

Comparison of condition factors at day 1 and day 10 of chinook control fish not exposed to the glochidia of *M. m. falcata*.

Fish No.	No. Parasites Attached	C.F. Day 1	C.F. Day 10	C.F. increase-decrease
1	0	1.34	1.29	- 3%
2	0	1.20	1.08	-10%
3	0	1.19	1.19	0%
4	0	1.22	1.20	- 2%
5	0	1.12	1.12	0%
6	0	1.44	1.44	0%
7	0	1.18	1.14	- 3%
8	0	1.34	1.34	0%
9	0	1.20	1.11	- 7%
10	0	1.30	1.35	+ 4%

Comparison of condition factors at day 1 and day 10 of coho control fish not exposed to the glochidia of *M. m. falcata*.

Fish No.	No. Parasites Attached	C.F. Day 1	C.F. Day 10	C.F. increase-decrease
1	0	1.20	1.30	+ 4%
2	0	1.42	1.09*	- 23%
3	0	1.51	1.68	+ 10%
4	0	1.56	1.71	+ 9%
5	0	1.38	1.57	+ 12%
6	0	1.44	1.44	0%
7	0	1.25	1.25	0%
8	0	1.66	1.79	+ 7%
9	0	1.44	1.44	0%
10	0	1.59	1.74	+ 9%

* Died before day 10.

Comparison of condition factors at day 1 and day 10 of steelhead control fish not exposed to the glochidia of *M. m. falcata*.

Fish No.	No. Parasites Attached	C.F. Day 1	C.F. Day 10	C.F. increase-decrease
1	0	1.01	2.03	+ 50%
2	0	1.39	1.94	+ 29%
3	0	1.52	2.03	+ 25%
4	0	1.64	1.43	- 12%
5	0	0.82	1.64	+ 50%
6	0	1.70	1.70	0%
7	0	1.03	2.04	+ 33%
8	0	1.17	1.89	+ 25%
9	0	0.92	1.94	+ 40%
10	0	0.91	0.91	0%